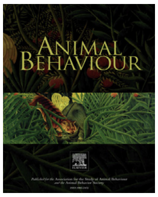
Animal Behaviour 137 (2018) 169–177

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav



Experimental manipulation of incubation period reveals no apparent costs of incubation in house wrens

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ARTICLE INFO

Article history:
Received 31 August 2017
Initial acceptance 27 September 2017
Final acceptance 23 November 2017
Available online 19 February 2018
MS. number: A17-00705

Keywords:
bird
cost of reproduction
incubation
life-history trade-offs
Troglodytes aedon

Fitness costs of incubation ensue whenever the trade-off between incubation and foraging leads to suboptimal incubation or decreased parental body condition. We examined the costs of incubation in a wild population of house wrens, *Troglodytes aedon*, by experimentally extending or decreasing the incubation period by cross-fostering eggs between nests at different stages of incubation (eggs from control nests were cross-fostered at the same stage of incubation). We determined whether parents or offspring bear the costs of incubation by measuring effects on females and offspring within the same breeding season during which the manipulation occurred, but also by evaluating potential trade-offs between current and future reproduction by monitoring return rates of experimental females and recruitment rates of offspring in subsequent breeding seasons. There was no difference in hatching or fledging success across treatments. There was also no effect of incubation duration on female size-corrected mass, and females from different treatments were equally likely to produce a second brood. Nestlings produced by control and experimental females did not differ in body mass, tarsus length or residual mass. Neither return rates of females, nor the number of offspring recruited, differed across treatments. We conclude, therefore, that although prolonged incubation entails increased energy expenditures, females are able to offset these losses while foraging, thereby mitigating the costs of incubation. This resiliency is more likely to be seen in income breeders, such as house wrens, that retain some ability to recoup energy expended in incubation, than in capital breeders that are constrained by stored energy reserves.

Incubation, once regarded as a relatively innocuous stage of avian reproduction, often entails significant energy expenditures (Nord & Williams, 2015). Incubating birds must meet these energetic demands either by foraging or by using stored energy reserves (Reid, Monaghan, & Nager, 2002). Income breeders, individuals that adjust their food intake according to their immediate needs (Drent & Daan, 1980; Jönsson, 1997), must balance the time spent foraging against the time required to maintain optimal incubation temperatures (Hepp, DuRant, & Hopkins, 2015). Fitness costs of incubation ensue, therefore, whenever the trade-off between incubation and foraging leads to suboptimal incubation or decreased parental body condition (Reid et al., 2002). Although this trade-off is widely believed to exact a significant cost of reproduction, any such cost can only be revealed through experimental manipulation of the energy required for incubation, or the amount of food available to incubating birds (Reid et al., 2002).

Various types of manipulations have been employed to explore the trade-off between incubation and foraging, among them, experimental manipulation of clutch size, altering the energy required for incubation by heating or cooling the nest, providing supplementary food or experimentally extending the period of incubation (reviewed in Reid et al., 2002). Of these, arguably the most widely used is an experimental increase in clutch size, predicated on the well-founded assumption that larger clutch sizes require greater energy expenditures during incubation (Tinbergen & Williams, 2002). Any decrease in hatching success or increase in the incubation period upon such an increase is often taken as evidence of a cost of reproduction associated with incubation (reviews in Reid et al., 2002; Thomson, Monaghan, & Furness, 1998), but such an inference can be misleading. Parents may be physically constrained in their ability to optimally incubate their eggs by the increased surface area presented by an enlarged clutch (Reid et al., 2002; Reid, Monaghan, & Ruxton, 2000a).

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https://doi.org/10.1016/j.anbehav.2018.01.006

Heating or cooling of the nest can be a particularly effective means to decrease or increase the energetic demands of incubation, respectively. Experimental heating of nests has been shown to result in decreased incubation effort, higher offspring body condition and greater fledging success (Pérez, Ardia, Chad, & Clotfelter, 2008; Reid, Monaghan, & Ruxton, 2000b), whereas experimental cooling of nests can lead to extended incubation periods and lower offspring body condition (Ardia, Pérez, & Clotfelter, 2010; Nilsson, Stjernman, & Nilsson, 2008). Although these results are consistent with a trade-off between incubation and foraging, other studies report opposing effects of heating (or cooling) on incubation effort (reviewed in Álvarez & Barba, 2014). Moreover, experimental heating or cooling does not always affect nestling development or condition (Álvarez & Barba, 2014), suggesting that under normal conditions, incubating parents may be able to offset energy expenditures during incubation while foraging off the nest, while still managing to maintain adequate incubation temperatures.

The provision of supplemental food to incubating birds offers another means of altering the presumed trade-off between incubation and foraging, the primary expectation being that increased availability of food should lead to an increase in incubation effort as the need to forage is correspondingly reduced. Although this basic expectation has been met in several studies (e.g. Barnett & Briskie, 2010; Chalfoun & Martin, 2007; Pearse, Cavitt, & Cully, 2004), a critical test of the presumed trade-off requires that greater incubation attentiveness actually enhances reproductive performance of the supplemented parent or some aspect of offspring fitness. Studies on house wrens, *Troglodytes aedon*, suggest that this does not always follow (Lothery, Thompson, Lawler, & Sakaluk, 2014; Pearse et al., 2004).

Arguably the most direct way of probing the costs of incubation is to force incubating individuals to alter their incubation effort by manipulating the length of the incubation period, which can be accomplished by cross-fostering eggs at different stages of embryonic development (Reid et al., 2002). A review of such cross-fostering experiments (Verhulst & Nilsson, 2008) reveals that parents with shortened incubation periods generally produce nestlings that grow faster, fledge at higher body mass and are more likely to recruit to the breeding population than those produced by parents forced to incubate for longer periods. Although these results are consistent with the hypothesis that incubation imposes significant costs of reproduction, their interpretation is obscured by a potential confound with the effects of time of season on reproductive performance (Brinkhof, Cavé, Daan, & Perdeck, 2002; Verhulst & Nilsson, 2008). The reproductive success of birds breeding in seasonal environments typically declines over the course of the season (Verhulst & Nilsson, 2008), so that any differences in reproductive success of individuals experiencing experimentally manipulated incubation periods could be due as much or more to a seasonal effect than to any effect of incubation effort per se. Consequently, great care must be taken in establishing appropriate controls with which to compare reproductive performance of birds with experimentally delayed and experimentally advanced hatching dates.

House wrens are an ideal study species with which to investigate costs of reproduction because females are easily manipulated into laying more eggs than they normally would (Bowers, Sakaluk, & Thompson, 2012; Hodges, Bowers, Thompson, & Sakaluk, 2015), and thus it is possible to manipulate each stage of the reproductive cycle independently of the other stages. These studies have revealed that the costs of increased egg production fall most heavily on the females, which are less likely to reproduce again (or at a lower reproductive output than control females; Bowers & Sakaluk, et al., 2012), whereas the costs of rearing supernumerary young appear to fall most heavily on the nestlings, which fledge at a lower body mass or lower body condition (Bowers, Nietz, Thompson, & Sakaluk, 2014; Finke, Milinkovich, & Thompson, 1987; but see Harper, Juliano, & Thompson, 1992). The costs of incubation are, however, less clear. An experimental increase in clutch size resulted in a slight increase in the incubation period, but no effect on hatching success or early nestling survival (Baltz & Thompson, 1988; Dobbs, Styrsky, & Thompson, 2006). Supplemental feeding of females during incubation increased nest attentiveness (Lothery et al., 2014; Pearse et al., 2004), but had no effect on female condition or reproductive success (Lothery et al., 2014).

Here we examine the costs of incubation in a wild population of house wrens by experimentally extending or decreasing the incubation period by cross-fostering eggs between nests at different stages of incubation. We attempted to determine whether parents or offspring bear the costs of incubation by measuring effects on females and offspring not only within the same breeding season during which the manipulation occurred, but also by evaluating potential trade-offs between current and future reproduction by monitoring return rates of experimental females and recruitment rates of offspring in subsequent breeding seasons. We predicted that if there is a trade-off between incubation and foraging, females forced to incubate for longer periods should have lower reproductive success than control females, whereas females incubating over experimentally shortened periods should enjoy higher reproductive success.

METHODS

House wrens are small (10–12 g), insectivorous songbirds and, as secondary cavity nesters, readily nest in nestboxes. Upon arrival at our study area in north-central Illinois (40°40′N, 88°53′W) following spring migration, females select a male in attendance at a nestbox and, after completing the nest, lay a clutch of four to eight eggs. In our study population, house wrens are double-brooded, with approximately half of the females producing a second brood within the same breeding season (Bowers & Sakaluk, et al., 2012; Bowers & Smith, et al., 2012; Drilling & Thompson, 1991). Only females incubate the eggs and brood the nestlings, but both adults provision nestlings and fledglings. Parents bring one prey item back to the nest at a time (Barnett, Clairardin, Thompson, & Sakaluk, 2011; Barnett, Thompson, & Sakaluk, 2012). Additional information concerning the breeding biology of house wrens is provided in Johnson (2014).

This study was initiated during the 2014 breeding season, with survival and reproductive success of experimental individuals monitored through the end of the 2016 breeding season. In all 3 years, we captured and banded nearly all the adults and nestlings produced on the study area. Nestboxes ($N = 820$) of uniform construction (Lambrechts et al., 2010) were spaced 30 m apart along north–south transects separated by 60 m. All nestboxes were mounted on 1.5 m metal poles and protected with 48.3 cm diameter aluminium baffles mounted below nestboxes to discourage terrestrial nest predators. We visited nestboxes twice weekly to determine the beginning of nest building and, once egg laying had begun, visited active nests daily until clutch completion. We deemed incubation to have begun when the clutch size remained the same over two consecutive days and the eggs were warm to the touch. Adults were captured inside nestboxes or by employing mist nets near the box during incubation or shortly after hatching, and uniquely banded with a U.S. Geological Survey leg band; in addition, males received three coloured bands in a unique combination to visually identify and distinguish them from females during provisioning.

Females normally incubate eggs for 12–13 days before they hatch. In 2014, we experimentally extended or decreased this